WATER-VAPOR LOSS FROM PLANTS GROWING IN VARIOUS HABITATS[1]

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A plant's external and internal water relationships have been used extensively in explaining plant distribution. For more than a century botanists have measured transpiration from plants in various ways, resulting in a vast accumulation of data. However, most such measurements have been on plants growing in an environment quite different from that of their native habitats. It seemed desirable to make an extensive study of water-vapor loss from leaves of plants as they were growing in various plant associations. The habitats selected for this study were typical of the Deciduous Forest Formation of the Central States. These observations were made chiefly in Ohio and a few in the central part of Indiana, during the summers of 1927 to 1931 inclusive. The data presented were obtained from determinations upon one hundred and forty-eight species, belonging to sixteen plant associations.

The writer desires to take this opportunity to express his appreciation to Dr. E. N. Transeau, under whose direction this work was planned and carried out.[2]

METHOD USED

Determinations of the rate of water-vapor loss were made with standardized cobalt chloride hygrometric paper. This method was selected because it can be so readily applied to plants under field conditions. The measurements obtained are thought to be sufficiently accurate for problems in physiological ecology. The cobalt chloride method was originated by Stahl (10), later improved by Livingston (5), Bakke (1), Livingston and Shreve (6), and finally by Meyer (7). The hygrometric paper used in the following experiments was standardized quantitatively by Meyer's method.

[1]Papers from the Department of Botany, The Ohio State University, No. 344.
[2]This paper represents a portion of the dissertation offered as a partial requirement for the doctorate degree from The Ohio State University.

The cobalt chloride hygrometric paper was prepared and mounted on narrow strips of celluloid as suggested by Meyer. The paper was cut into discs $^{15}/_{32}$ inches in diameter and fastened to each end and on the same surface of the strips, by means of gummed reenforcements for notebook paper. These held the hygrometric paper pieces in position with only the one surface exposed, which was to be placed next to the leaf to be tested, and the other surface could be seen through the celluloid. The strips were then folded along the short axis through the center. This made a clip which could be readily clamped to a leaf with the sensitive paper exposed to each epidermal surface. Small clamps (Dennison's Card Holder No. 42) were found satisfactory for holding the clip in place on the leaf.

Small desiccators for drying the clips were made from 100 cc. wide-mouthed bottles, stoppered with paraffined corks. Anhydrous calcium chloride was used as the desiccating agent. Cotton was placed on top of the calcium chloride to prevent the paper from coming in contact with the calcium.

It should be emphasized that the method does not measure transpiration as it normally occurs, but it does measure water-vapor loss under a standard set of conditions. For this reason the water-vapor loss as measured by the cobalt chloride paper has been called "standard water-vapor loss" by both Meyer (7) and Blaydes (2).

It may be well to point out some of the conditions of the artificial environment produced by the hygrometric paper clips. When a clip is applied to a leaf, light is removed from that small area under the clip into which water-vapor is lost by the leaf. Wind can have no direct effect on the small portion of the leaf being tested. All measurements may be reduced to a standard temperature by Livingston and Shreve's (6) method. Humidity of the atmosphere about the leaf has little if any direct effect, for almost as soon as the desiccated hygrometric paper is applied to the leaf, the small space between the clip and the leaf registers close to zero humidity. Therefore, the leaf surface being tested at first loses water-vapor to a nearly desiccated atmosphere. As the determination continues, however, this atmosphere becomes more and more humid. This introduces some error since the diffusion gradient is gradually decreased. The results of measurements of the water loss from a plant living in a very humid environment will deviate more from true transpiration rate than will the result of such measurement upon plants in a dry environment. That is, the water-vapor loss as measured is more nearly a determination of what the plant would lose under the drier condition of the atmosphere. Blaydes (3) has shown that amounts obtained by the cobalt chloride hygrometric paper method and the weighing method do not necessarily coincide.

STANDARD WATER-VAPOR LOSS MEASUREMENTS

The objective of this work was to determine whether the standard water-vapor loss from plants of various associations was an adequate measure or an indicator of the habitat, as far as water relations were concerned. Livingston (5) and Bakke (1) concluded that the cobalt chloride hygrometric paper measurements might be used as indices of a given plant's water relations. Bakke also believed that the indices determined offered a comparatively simple and adequate method for classifying plant forms in a scale of xerophytism or mesophytism. Pool (8) studied forty representative species found in various plant communities from the short-grass mesas and plateaus east of Colorado Springs and up through the foothill bushlands to the subalpine forest associations, and the alpine meadows above an altitude of 12,000 feet. He determined the indices of "transpiring power," beginning with the most xerophytic forms and closing with the more mesophytic. In addition he made an anatomical study of the leaves of representative species and found that some species with strikingly xeromorphic leaves showed relatively high indices of "transpiring power." The indices for dominants and other species of various communities did not show very satisfactory differentiation of habitats. Wilson (12), working upon transplanted plants, found that the so-called xerophytes of Australia, "so long as the available water supply is adequate, have no special powers of accommodation," as far as transpiration is concerned. Meyer (7) studied eight woody species in Ohio and states "it is doubtful if the standard rate of water-vapor loss from the leaves of a species may be taken as an adequate criterion of the relative mesophytism or xerophytism of that species."

It will be noted that the data to be presented were obtained in habitats of entirely different plant formations from those studied by Livingston (5), Bakke (1) and Pool (8), but in the same as those of Meyer. Instead of isolated measurements made on each plant as those of Livingston, Bakke and Pool and attempts at correlation with the habitat, these data represent a series of measurements made on each plant, at hourly intervals during a considerable part of the daylight period. It was expected that the more complete measurements would be more likely to show whether or not a correlation between habitat and rate of water-vapor loss existed.

It should be emphasized again that it is not likely that accurate comparisons of relative transpiration rates are possible between the plants growing on a dry, exposed hilltop and plants growing in a very moist habitat; or between herbaceous plants on the forest floor and exposed leaves of the tree cover. However, the standard water-vapor loss of plants of the two situations can be accurately compared.

In all cases the species selected for the tests are fairly representative of the given association. Leaves were selected which were apparently of the same age, size and condition. For each species, tests were made on five different leaves and the results averaged. Thus each figure on the following graphs represents the average of five approximately simultaneous measurements. The temperature was standardized to 20° C. for all the tests by Livingston and Shreve's (6) method. The standard water-vapor loss is given in terms of grams or fractions thereof, on the ordinates. The time representing daylight hours is shown on the abscissae.[3] The legend accompanying the graphs denotes the association in which the plants were growing, the date upon which the measurements were made, and the name of the plant. Usually two species were measured during a given day. These two were growing close together and living under very similar environmental conditions, except where type of root systems varied. Graphs for these may be identified by the dates given, if comparisons are desired. The nomenclature used is that of Gray (4).

An analysis of the data presented shows that in practically all species where no stomata are present on the upper surface of the leaves, the cuticular loss is 0.3 gram or less per hundred square centimeters of leaf surface per hour. This value is approximately the same whether the plant is growing in a dry habitat such as Oak-Cedar Cliffs association, in a Chestnut-

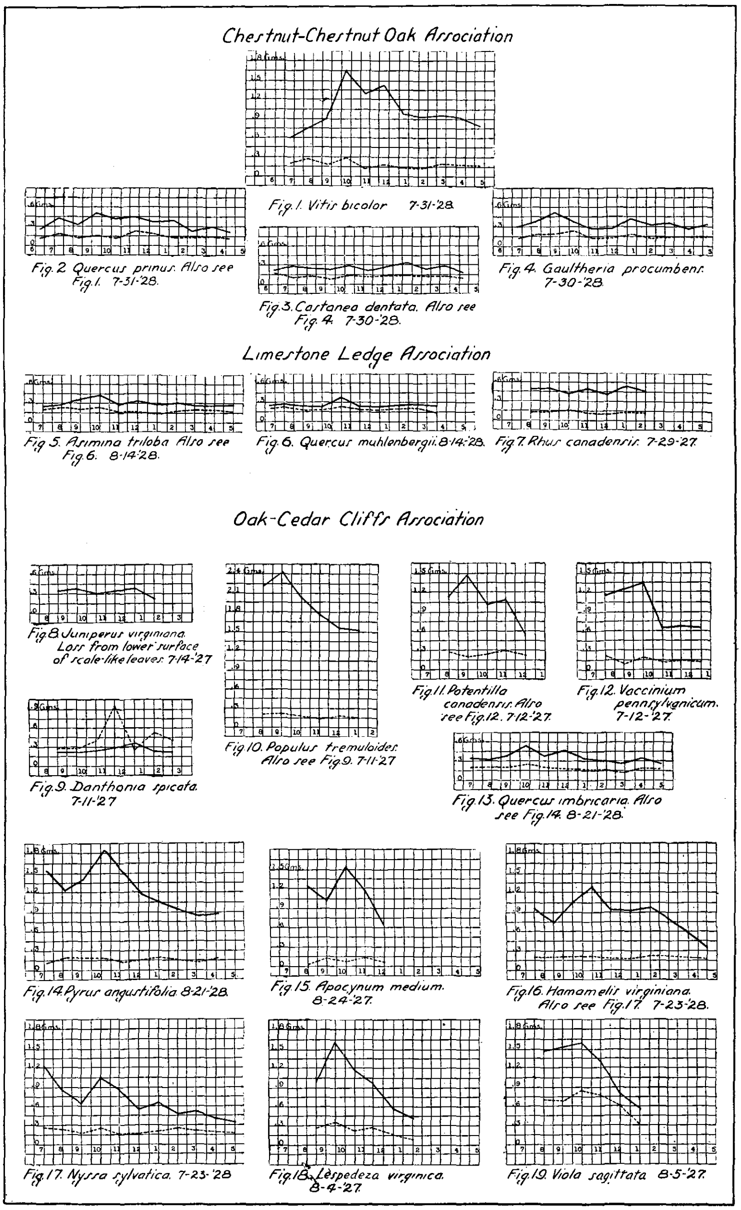
[3]Dotted lines of graphs (Figs. 1-119) indicate water vapor-loss from upper leaf surfaces, and solid lines loss from lower surfaces.

Chestnut Oak habitat, in a moist situation such as Buttonbush Swamp, or on a Sandbar.[4]

In the most xeric habitats studied, namely, the Chestnut-Chestnut Oak and the Limestone Ledge associations, the water-vapor loss from the surfaces bearing stomata was but little greater than stomata free surfaces. A decided exception is *Vitis bicolor* (Fig. 1), which was growing very near *Quercus prinus* (Fig. 2). *V. bicolor* is characteristic of the Chestnut-Chestnut Oak situation in Ohio. The measurements on the two plants were taken almost simultaneously (half hour apart). The water-vapor loss of the *V. bicolor* had a much greater maximum (1.7 g.), and in general, the whole water loss curve is greater than that of *Vitis cordifolia* (maximum, 1.1 g.) (Fig. 86), a typical River Bank form. Incidentally, a comparison of these two is also of interest since the leaves of *V. bicolor* are quite hairy while those of *V. cordifolia* are glabrous. This again emphasizes the fact that epidermal hairs are of no importance in retarding water-vapor loss, agreeing with Sayre's results for *Verbascum* (9). A comparison between the water losses of these two species of grape also indicates that a species typical of a dry habitat may lose water-vapor more rapidly than a typical species of a constantly moist habitat. Possibly internal conditions are of greater importance in determining the type of water loss than the amount of available water in the soil.

In the Oak-Cedar Cliffs association some comparatively high water losses are recorded. This particular region is underlaid with Ohio Black Shale from which considerable seepage occurs in deep ravines most of the year. *Populus tremuloides* (Fig. 10) showed an exceptionally high rate of water-vapor loss. *Quercus imbricaria* (Fig. 13) showed a very low rate. *Pyrus angustifolia* (Fig. 14) growing within a few feet of the oak was measured during alternate hours on the same day. A comparatively high rate of water loss was shown. *Danthonia spicata* (Fig. 9) is of interest since the greater loss is from the upper surface of the leaves. Loss from the lower surface is more nearly that found for cuticular surfaces. This species with *Juniperus* (Fig. 8) and *Quercus*, had the lowest rates of water-vapor loss among the twelve species studied. It is of

[4]For some associations, habitat names rather than standard plant association names have been used in order to indicate more specifically conditions in which the particular experimental plants were growing.



Chestnut-Chestnut Oak Association

Fig. 1. Vitis bicolor 7-31-'28.

Fig. 2. Quercus prinus. Also see Fig. 1. 7-31-'28.

Fig. 3. Castanea dentata. Also see Fig. 4. 7-30-'28.

Fig. 4. Gaultheria procumbens. 7-30-'28.

Limestone Ledge Association

Fig. 5. Asimina triloba. Also see Fig. 6. 8-14-'28.

Fig. 6. Quercus muhlenbergii. 8-14-'28.

Fig. 7. Rhus canadensis. 7-29-'27.

Oak-Cedar Cliffs Association

Fig. 8. Juniperus virginiana. Loss from lower surface of scale-like leaves. 7-14-'27.

Fig. 9. Danthonia spicata. 7-11-'27.

Fig. 10. Populus tremuloides. Also see Fig. 9. 7-11-'27.

Fig. 11. Potentilla canadensis. Also see Fig. 12. 7-12-'27.

Fig. 12. Vaccinium pennsylvanicum. 7-12-'27.

Fig. 13. Quercus imbricaria. Also see Fig. 14. 8-21-'28.

Fig. 14. Pyrus angustifolia 8-21-'28.

Fig. 15. Apocynum medium. 8-24-'27.

Fig. 16. Hamamelis virginiana. Also see Fig. 17. 7-23-'28.

Fig. 17. Nyssa sylvatica. 7-23-'28.

Fig. 18. Lespedeza virginica. 8-4-'27.

Fig. 19. Viola sagittata. 8-5-'27.

interest to compare the loss from *Danthonia* with that of *Viola* (Fig. 19). These two plants grew side by side, and both are shallow-rooted forms.

The Cliff Crevice association types showed no great extremes of water-vapor loss. It is probable that such forms experience at least short extreme droughts due to the small accumulations of soil. Probably all species have been eliminated excepting forms which can withstand such dry periods.

Acer saccharum (Fig. 25), one of the dominants of the Beech-Maple habitat, showed a loss which might have been expected in a more xeric situation; in fact the curve is very similar to *Castanea* (Fig. 3), *Gaultheria* (Fig. 4), and *Quercus prinus* (Fig. 2), of the Chestnut-Chestnut Oak association. The similarity of the curves for *Asimina triloba* (Fig. 5), *Quercus muhlenbergii* (Fig. 6), and *Rhus canadensis* (Fig. 7), of the Limestone Ledge association, which was very dry, is also quite apparent. On the other hand, *Tradescantia pilosa* (Fig. 31) and *Smilax rotundifolia* (Fig. 30), of the Beech-Maple habitat, were in the group of highest water-vapor losing species found. *Ribes cynosbati* (Fig. 34), growing within a few feet of the others, showed a low rate of loss, approaching that of *Acer*. *Arisaema* (Fig. 28) and *Asarum* (Fig. 32) showed a water-loss curve which falls between the high and low water losers of the habitat. The graphs for these two are also strikingly similar. The loss curve for *Sanguinaria* (Fig. 33) is of interest in comparison to these last two since it is an herbaceous, early spring form and approaches *Acer* and *Ribes* in its type of water loss. The habitat of these Beech-Maple forms was very moist at the time measurements were made, due to a preceding thirty day period during which time rain fell almost every day. *Scrophularia* (Fig. 38), *Juglans* (Fig. 35), and *Aster* (Fig. 36), were growing in a more open place within the Beech-Maple habitat. Measurements on these species were made during a much drier period. These three showed water-loss curves having well marked periodicity with the maxima during the morning hours.

The Beech Forest association is very similar to the Beech-Maple community. Poorer drainage, probably, is the condition which eliminates the maples. Excepting *Fagus* (Fig. 41), all the species measured in this situation were forms not tested in the Beech-Maple situation. In general, the loss curves are similar to those of the related community. Growing within

Cliff Crevice Association

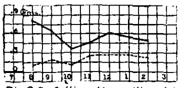


Fig. 20. Sullivantia sullivantii. Also see Fig. 22. 8-17-'27

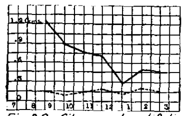


Fig. 22. Silene rotundifolia. 8-17-'27.

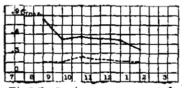


Fig. 23. Asplenium pinnatifidum 8-18-'27.

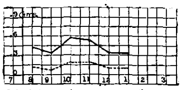


Fig. 21. Hydrangea arborescens. Also see Fig. 23. 8-18-'27.

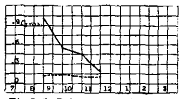


Fig. 24. Pilea pumila 8-19-'27

Beech-Maple Association

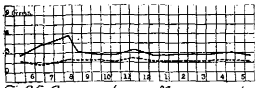


Fig. 25. Acer saccharum. Measurements made at height of twenty feet. 7-2-'28

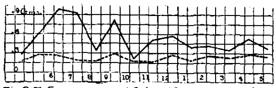


Fig. 27. Fagus grandifolia. Measurements made on same tree as for Fig. 26, and at a height of thirty feet. 7-19-'28.

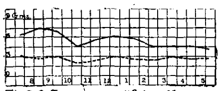


Fig. 26. Fagus grandifolia. Measurements made at a height of about four feet. 7-16-'28.

Fig. 28. Arisaema triphyllum. Also see Fig. 29. 7-3-'28.

Fig. 29. Menispermum canadense. 7-3-'28.

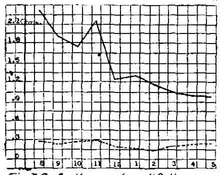


Fig. 30. Smilax rotundifolia. Also see Fig. 31. 7-6-'28.

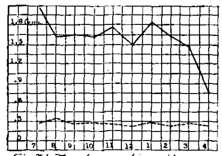


Fig. 31. Tradescantia pilosa. 7-6-'28.

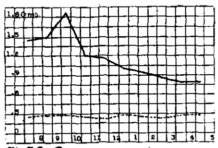


Fig. 32. Asarum canadense. 7-7-'28.

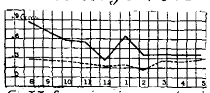


Fig. 33. Sanguinaria canadensis. Also see Fig. 34. 7-25-'28.

Fig. 35. Juglans nigra. Also see Fig. 38. 8-20-'28.

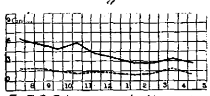


Fig. 34. Ribes cynosbati. 7-25-'28.

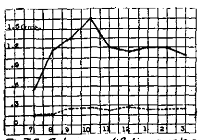


Fig. 36. Aster cordifolius. 8-16-'28.

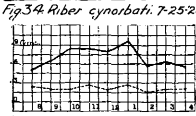


Fig. 37. Carya cordiformis. Also see Fig. 36. 8-16-'28.

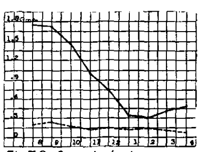


Fig. 38. Scrophularia marilandica. 8-20-'28.

a few feet of each other, the curves for *Fagus* and *Cornus* (Fig. 42) are similar. However, the maxima are rather widely separated. The curves for *Circaea* (Fig. 39) and *Actea* (Fig. 40) which grew side by side are also paralleled.

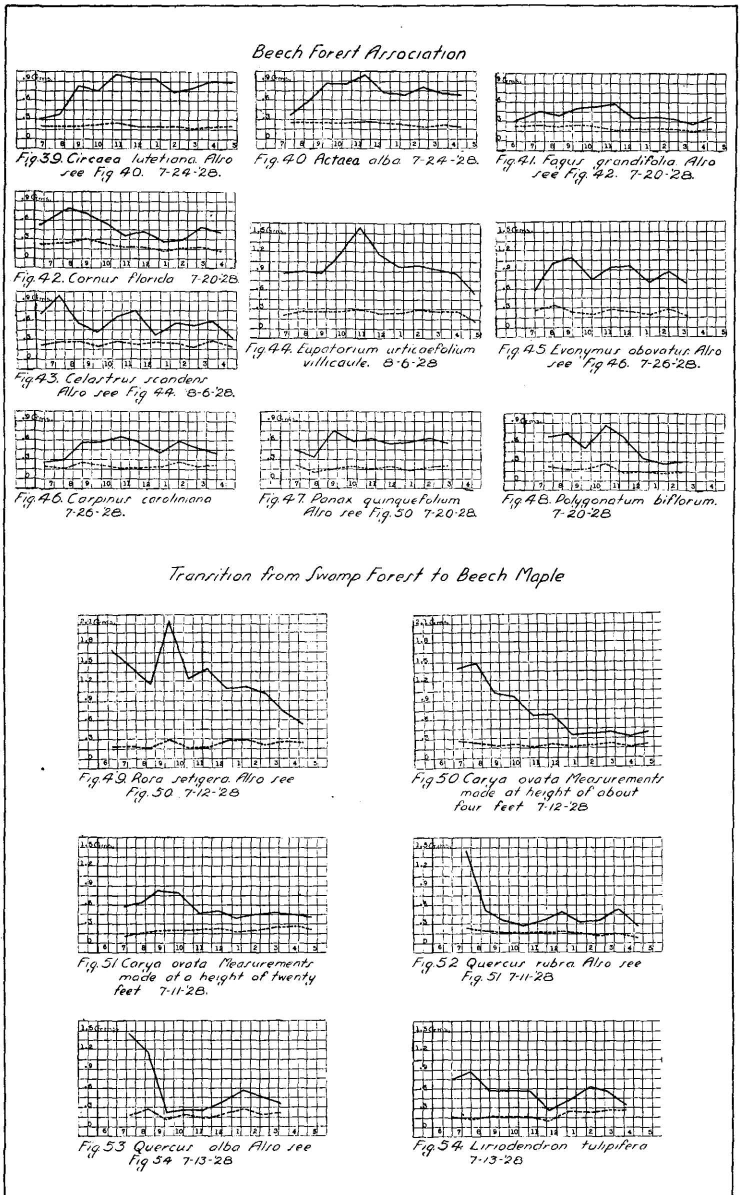
Among the species studied in a transition between Swamp Forest and Beech-Maple no unusual departures were found except among the Oaks. *Quercus alba* (Fig. 53) and *Q. rubra* (*borealis*) (Fig. 52) showed high maxima in the early morning. This did not appear previously in the species of *Quercus* from apparently drier habitats.

Species of the Swamp Forest habitat show a wide range of variation in rates of water loss. The highest loss observed (2.9 g. per sq. dm.) during this investigation was that recorded for *Lobelia cardinalis* (Fig. 62). *Quercus macrocarpa* (Fig. 56) and *Q. bicolor* (Fig. 55) showed water loss curves which were quite similar to oaks of more xeric habitats. *Quercus palustris* (Fig. 63) approaches the average for this association.

Graphs of several of the Flood Plain species are short due to a very rainy season, and to nights with low temperatures and heavy dews. This prevented the early morning measurements. *Fraxinus americana* (Fig. 68) and *Prunus serotina* (Fig. 69), growing side by side, with the measurements taken upon alternate hours, show similar curves, and *Pilea pumila* (Fig. 65) compared with the same species growing in the Cliff Crevice association (Fig. 24) shows a higher and a later maximum.

In the Mixed Mesophytic Forest, *Betula lenta* (Fig. 81) and *Cimicifuga racemosa* (Fig. 79) were the only species measured which showed a comparatively high water-vapor loss. The curve for *Fagus* (Fig. 83), *Oxydendron* (Fig. 80), *Kalmia* (Fig. 82), and *Rhododendron* (Fig. 78) approach those found commonly in drier situations. In south central Ohio, *Kalmia* is usually found on dry ridges. The water-vapor loss from it, however, is greater than from *Rhododendron*. Meyer (7) observed the same phenomenon. The time of greatest water loss for the *Rhododendron* occurred early in the morning, as previously reported by Meyer. *Kalmia* occurs abundantly on the very dry sandstone cliff-tops in southern Ohio, while *Rhododendron* is closely restricted to the moist ravines and north-facing slopes.

The River Bank forms show a rather wide range of fluctuations. They are more or less characterized by high, sudden maxima and rapid declines.



Beech Forest Association

Fig. 39. Circaea lutetiana. Also see Fig 40. 7-24-28.

Fig. 40 Actaea alba 7-24-28.

Fig. 41. Fagus grandifolia. Also see Fig. 42. 7-20-28.

Fig. 42. Cornus florida 7-20-28.

Fig. 43. Celastrus scandens Also see Fig 44. 8-6-28.

Fig. 44. Eupatorium urticaefolium villicaule. 8-6-28

Fig. 45 Evonymus obovatus. Also see Fig 46. 7-26-28.

Fig. 46. Carpinus caroliniana 7-26-28.

Fig. 47. Panax quinquefolium Also see Fig. 50 7-20-28.

Fig. 48. Polygonatum biflorum. 7-20-28

Transition from Swamp Forest to Beech Maple

Fig. 49. Rosa setigera. Also see Fig. 50 7-12-28

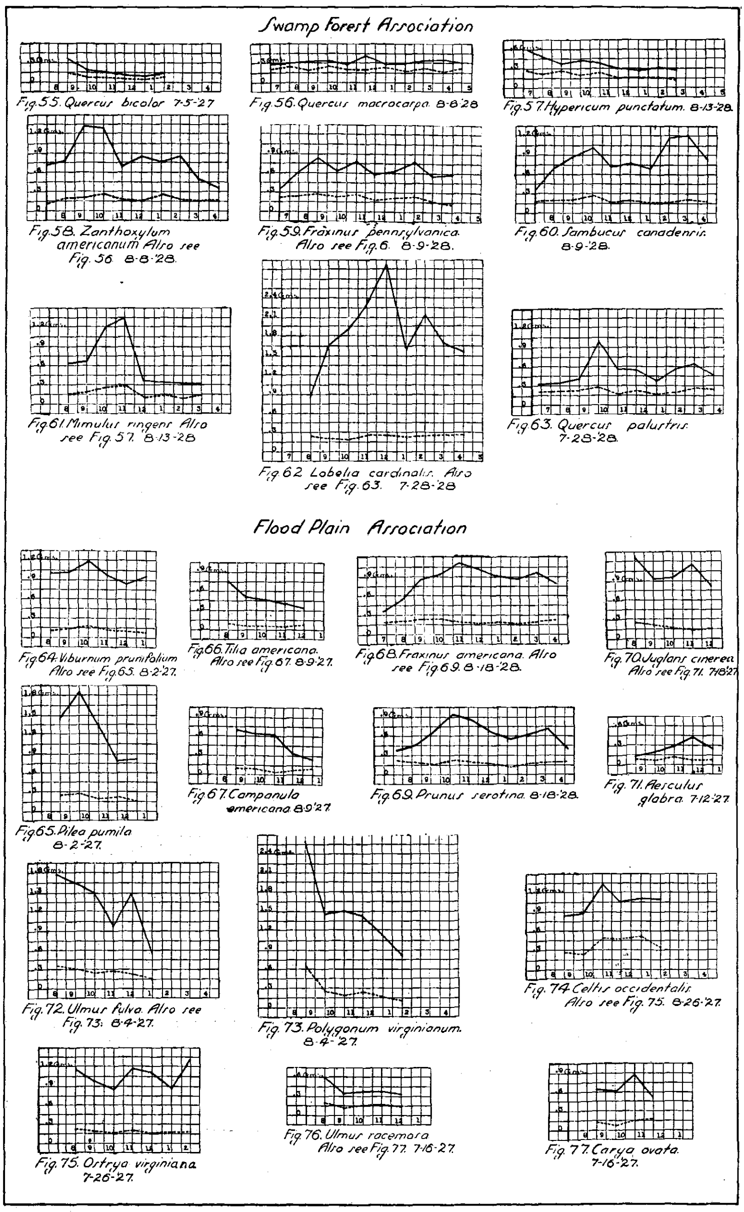
Fig. 50 Carya ovata Measurements made at height of about four feet 7-12-28

Fig. 51 Carya ovata Measurements made at a height of twenty feet 7-11-28.

Fig. 52 Quercus rubra. Also see Fig. 51 7-11-28

Fig. 53 Quercus alba Also see Fig 54 7-13-28

Fig. 54 Liriodendron tulipifera 7-13-28


Swamp Forest Association
Fig. 55. Quercus bicolor 7-5-27
Fig. 56. Quercus macrocarpa. 8-8-28
Fig. 57. Hypericum punctatum. 8-13-28.
Fig. 58. Zanthoxylum americanum Also see Fig. 56 8-8-28.
Fig. 59. Fraxinus pennsylvanica. Also see Fig. 6. 8-9-28.
Fig. 60. Sambucus canadensis. 8-9-28.
Fig. 61. Mimulus ringens Also see Fig. 57. 8-13-28
Fig. 62 Lobelia cardinalis. Also see Fig. 63. 7-28-28
Fig. 63. Quercus palustris. 7-28-28.
Flood Plain Association
Fig. 64. Viburnum prunifolium Also see Fig. 65. 8-2-27.
Fig. 66. Tilia americana. Also see Fig. 67. 8-9-27.
Fig. 68. Fraxinus americana. Also see Fig. 69. 8-18-28.
Fig. 70. Juglans cinerea. Also see Fig. 71. 7-18-27
Fig. 65. Pilea pumila 8-2-27.
Fig. 67. Campanula americana 8-9-27.
Fig. 69. Prunus serotina. 8-18-28.
Fig. 71. Aesculus glabra. 7-12-27.
Fig. 72. Ulmus fulva. Also see Fig. 73. 8-4-27.
Fig. 73. Polygonum virginianum. 8-4-27.
Fig. 74. Celtis occidentalis. Also see Fig. 75. 8-26-27.
Fig. 75. Ostrya virginiana 7-26-27.
Fig. 76. Ulmus racemosa Also see Fig. 77. 7-16-27.
Fig. 77. Carya ovata. 7-16-27.

Mixed Mesophytic Association

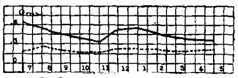


Fig. 78. Rhododendron maximum. 8-2-'28

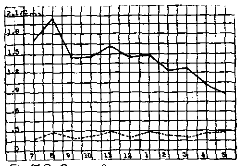


Fig. 79. Cimicifuga racemosa. 8-1-'28.

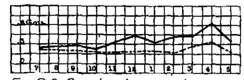


Fig. 80. Oxydendrum arboreum. Also see Fig. 81. 8-3-'28.

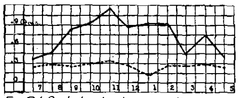


Fig. 81. Betula lenta. 8-3-'28

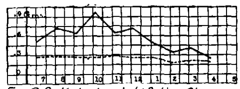


Fig. 82. Kalmia latifolia. Also see Fig. 83 8-4-'28.

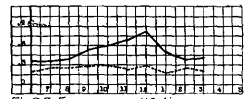


Fig. 83. Fagus grandifolia. 8-4-'28.

River Bank Association

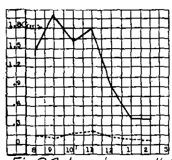


Fig. 84. Impatiens pallida. Also see Fig. 85. 8-1-'27.

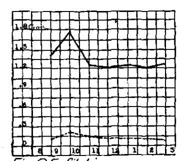


Fig. 85. Silphium perfoliatum 8-1-'27.

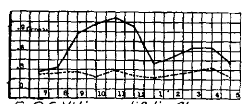


Fig. 86. Vitis cordifolia. Also see Fig. 87. 8-15-'28.

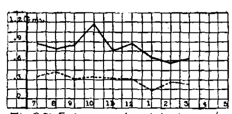


Fig. 87. Echinocystis lobata. 8-15-'28.

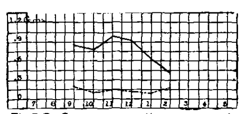


Fig. 88. Cinna arundinacea 7-28-'27.

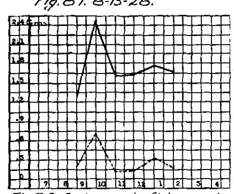


Fig. 89. Ambrosia trifida. 7-29-'27.

Sandbar Association

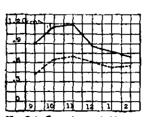


Fig. 90. Populus deltoides. Also see Fig. 91. 8-5-'27.

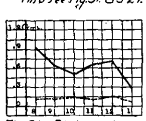


Fig. 91. Platanus occidentalis. 8-5-'27.

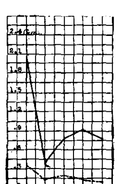


Fig. 92. Xanthium commune. Also see Fig. 93. 8-16-'27.

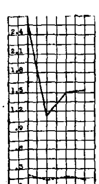


Fig. 93. Bidens frondosa. 8-16-'27

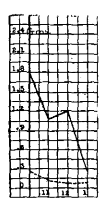


Fig. 94. Polygonum acre. Also see Fig. 95. 8-25-'27.

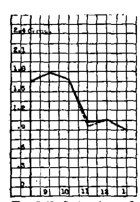


Fig. 95. Salix longifolia. 8-25-'27.

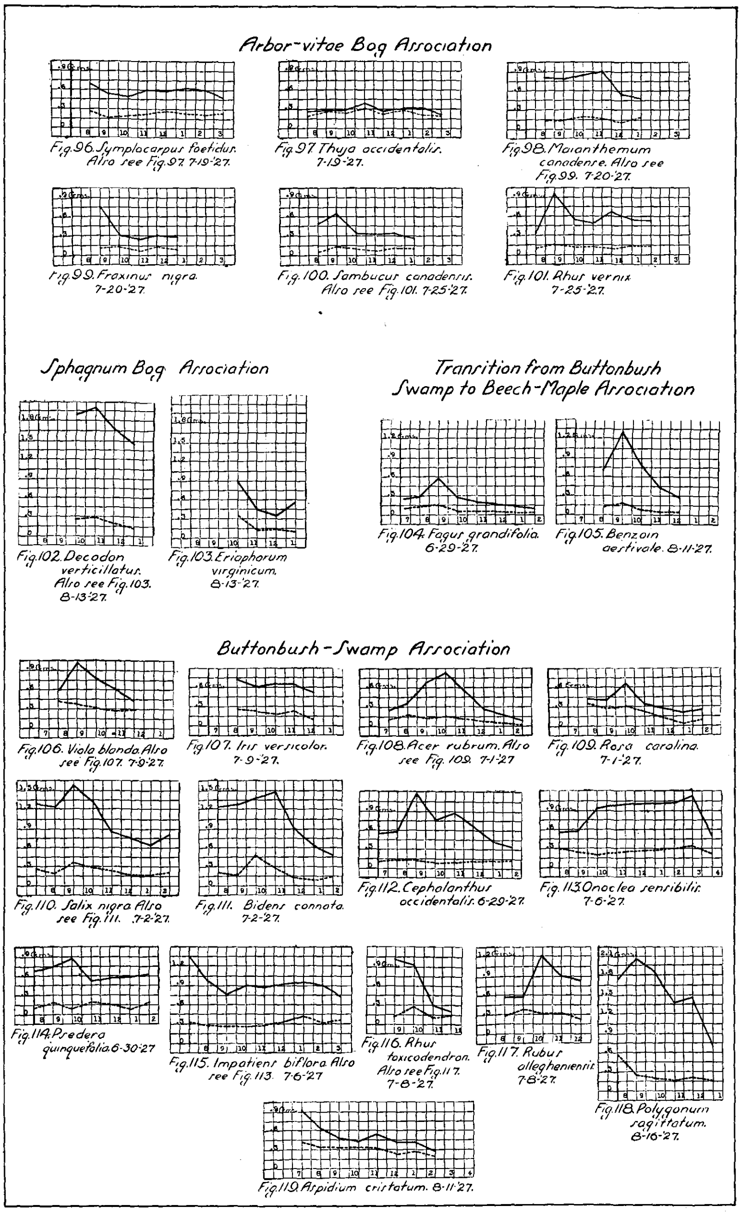
The Sandbar habitat species show high maxima at an early hour. Perhaps the graph for *Salix longifolia* (Fig. 95) is of some interest in that the losses from the two leaf surfaces are practically the same.

Representatives of the Arbor-vitae Bog association (alkaline) showed a relatively low rate of water-vapor loss. The curves for *Thuja* (Fig. 97) do not represent the upper and lower surfaces of the scale leaves, but the loss as measured from the upper and lower surfaces of the scale covered twigs. The soil is saturated with water in this situation practically the whole year. Root systems in such situations are usually poorly developed, due to lack of oxygen. This may account for the low rates obtained. Whitfield (11) concluded from his experiments with potted sunflowers that "Transpiration was found to be highest in soils of medium water content, next in saturated soils, and lowest in soils with low water content." *Sambucus* in this habitat (Fig. 100) has about half the rate of water loss of the same species (Fig. 60), growing in the Swamp Forest association.

Only two species of the Sphagnum Bog association (acid) were measured. The short curves are rather unsatisfactory, but do show two very different types of water-vapor loss: *Decodon*-high (Fig. 102), *Eriophorum*-low (Fig. 103).

The Buttonbush Swamp habitat is characterized by its saturated soil throughout the year. The water loss curves for the species in this situation are all low and much the same as in the Arbor-vitae Bog. One of the lowest was *Iris versicolor* (Fig. 107). It is common knowledge that this species grows well in much drier situations in cultivation. *Rosa carolina* (Fig. 109) showed the minimum water loss in the group. Its maximum was only .62 gram per unit area. Lack of available water cannot be the cause since the soil was saturated. *Fagus* (Fig. 104) and *Benzoin* (Fig. 105) represent the Transition Zone from Buttonbush Swamp to Beech-Maple; the first being low, the second, medium high.

The above analysis of the data presented indicates that the standard water-vapor loss of a species cannot be taken generally as an indicator of its xerophytic or mesophytic character. To make a separation on this basis would place many species of hydrophytic forms in xerophytic habitats where they rarely or never occur and *vice versa*. This indicates that the rate of standard water-vapor loss may be an important quality of the



Arbor-vitae Bog Association

Fig. 96. Symplocarpus foetidus. Also see Fig. 97. 7-19-'27.

Fig. 97. Thuja occidentalis. 7-19-'27.

Fig. 98. Maianthemum canadense. Also see Fig. 99. 7-20-'27.

Fig. 99. Fraxinus nigra. 7-20-'27.

Fig. 100. Sambucus canadensis. Also see Fig. 101. 7-25-'27.

Fig. 101. Rhus vernix 7-25-'27.

Sphagnum Bog Association

Fig. 102. Decodon verticillatus. Also see Fig. 103. 8-13-'27.

Fig. 103. Eriophorum virginicum. 8-13-'27.

Transition from Buttonbush Swamp to Beech-Maple Association

Fig. 104. Fagus grandifolia. 6-29-'27.

Fig. 105. Benzoin aestivale. 8-11-'27.

Buttonbush-Swamp Association

Fig. 106. Viola blanda. Also see Fig. 107. 7-9-'27.

Fig. 107. Iris versicolor. 7-9-'27.

Fig. 108. Acer rubrum. Also see Fig. 109. 7-1-'27

Fig. 109. Rosa carolina. 7-1-'27.

Fig. 110. Salix nigra Also see Fig. 111. 7-2-'27.

Fig. 111. Bidens connata. 7-2-'27.

Fig. 112. Cephalanthus occidentalis. 6-29-'27.

Fig. 113. Onoclea sensibilis. 7-6-'27.

Fig. 114. Psedera quinquefolia. 6-30-'27

Fig. 115. Impatiens biflora Also see Fig. 113. 7-6-'27

Fig. 116. Rhus toxicodendron. Also see Fig. 117. 7-8-'27.

Fig. 117. Rubus alleghenensis. 7-8-'27.

Fig. 118. Polygonum sagittatum. 8-16-'27.

Fig. 119. Aspidium cristatum. 8-11-'27.

plant in some cases and not in others, just as light intensity is important in the distribution of some species and not in others.

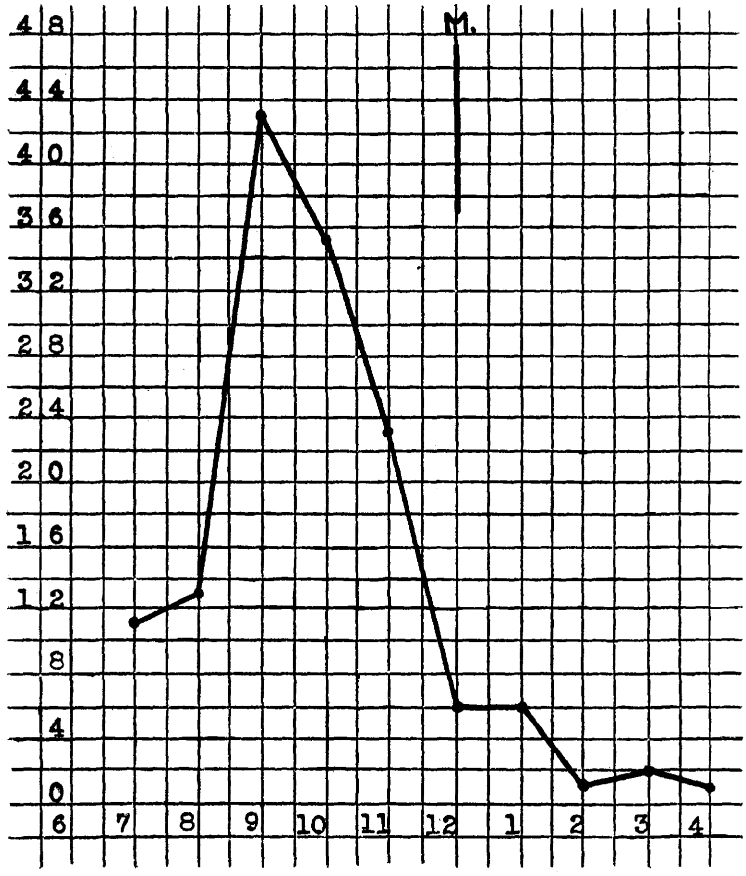


Fig. 120

FIG. 120. This graph shows the frequency of the water-vapor loss maxima for nine hours of the daylight period, collected from 148 plants growing in various habitats. Over 93% of the maxima occurred between 7:00 A. M. and 12:00 M.; 89% occurred between 7:00 and 11:00 A. M.; 52% occurred from 9:00 to 10:00 A. M. The maxima are given on the ordinate and time on the abscissa.

Early maxima are outstanding characteristics of most of the water-vapor loss graphs presented. From these maxima a a frequency curve (Fig. 120) has been constructed for nine hours of the daylight period.[5] Data from thirty other water-

[5]In order to make this graph more uniform, measurements occurring on the half hour have been placed with those of the following hour. Those falling between the hour and half hour have been placed with the nearest hour.

vapor loss curves, which have not been used otherwise in this paper, are included in this particular compilation. Plants from which these curves were made were cultivated varieties, weeds and additional wild forms used in investigating other water-vapor loss phenomena. Table I gives a list of these plants along with their time of maximum loss.

TABLE I

Name	Time of Maximum Water-Vapor Loss.
Asclepias syrica	11:00 A. M.
Canna flaccida	10:00 "
Growing in the greenhouse.	
Cannabis sativa	9:00 "
Bologna variety, staminate plant.	
Cannabis sativa	9:00 "
Bologna variety, carpellate plant.	
Cannabis sativa	10:00 "
Chington variety, staminate plant.	
Cannabis sativa	10:00 "
Chington variety, carpellate plant.	
Cannabis sativa	9:00 "
Commercial variety, staminate plant.	
Cannabis sativa	9:00 "
Commercial variety, carpellate plant.	
Cannabis sativa	9:00 "
Simple Leaf variety, staminate plant.	
Cannabis sativa	9:00 "
Simple Leaf variety, carpellate plant.	
Carica papaya	9:00 "
Growing in greenhouse.	
Commandra umbellata	9:00 "
Conocephalum conicum	10:00 "
Gametophyte.	
Diospyros virginiana	8:00 "
Measurements made July 10th.	
Diospyros virginiana	9:00 "
Same plant as above, but measured September 18th.	
Fraxinus caroliniana	11:00 "
Gossipium herbaceum	11:00 "
Melbane Big Bole Early Triumph.	
Helianthus tuberosus	10:00 "
Potted plant.	
Phaseolus vulgaris	1:00 P. M.
Measured August 20th.	
Phaseolus vulgaris	10:00 A. M.
Not the same as above. Measured August 16th.	
Phaseolus vulgaris	11:00 "
Seedling, measured September 3rd.	
Phaseolus vulgaris	10:00 "
Seedling, measured August 27th.	
Phoradendron flavescens	1:00 P. M.
Pyrus malus	9:00 A. M.
Grimes Golden variety. Measured July 10th.	
Pyrus malus	9:00 "
Same plant as above, but measured September 18th.	
Rhododendron maximum	12:00 M.
Leaves of second season.	
Sicyos angulatus	9:00 A. M.
Vaccinium pennsylvanicum	10:00 "

An analysis of this frequency curve of the water-vapor loss maxima determined for plants growing under various conditions, shows the percentage of maxima occurring between 7:00 A. M. to 12 M. to be over 93%; over 89% occurred between 7:00 to 11:00 A. M.; and 52% between 9:00 and 10:00 A. M. The greatest number of maxima (29%) occurred at 9:00 A. M. In other words, for over 93% of the plants studied, water-vapor loss maxima occurred before the period of maximum evaporation. An analysis of the maxima for each plant association shows that they are all quite variable within a given habitat, but that a majority in each location occurred before noon.

In practically all species studied, a distinct rhythm in the rate of water-vapor loss was very apparent. In some species the cuticular loss from the upper, stomata-free surfaces, showed slight rhythms.

It will be noted that measurements were made on *Fagus* (Figs. 27, 41, 83, 104) growing in four different habitats; *Sambucus* (Figs. 60, 100), *Carya ovata* (Figs. 50, 77), and *Pilea* (Figs. 24, 65), each growing in two different associations. As shown in these figures, the time of the maximum water-vapor loss, as well as the rhythms in general, varied from place to place.

Graphs are also presented showing the standard water-vapor loss from two different positions in the same tree. The species used were *Fagus* (Figs. 26, 27) and *Carya ovata* (Figs. 50, 51). The beech was measured at a height of thirty feet and again at approximately four feet. The lower position showed a higher maximum loss and a more pronounced rhythm. Measurements were made on the hickory at a height of twenty feet, and again at about four feet. The lower position showed a much higher maximum and, in general, a greater water-vapor loss.

SUMMARY

1. Determinations have been made of the standard water-vapor loss rates for 148 species of plants, representative of 16 plant associations located in the Deciduous Forest Formation of Ohio and Indiana.

2. Measurements were made, usually at hourly intervals, several times during the daylight period. This made possible the construction of curves showing diurnal variations in rate of water-vapor loss. This enables one to gain a more accurate idea of total daily standard water-vapor loss and its relation, if any,

to the habitat. Most other investigators of water loss have confined their determinations to isolated measurements. In many species the graphs show that the time of day may make a difference of 100% or more.

3. The standard water-vapor loss from herbaceous and low shrubs of the forest floor is often greater than the loss from lower leaves of plants forming the canopy. This conclusion is based upon comparisons of the loss of the forest floor types and the lower leaves of the canopy-forming trees. The atmospheric conditions about the lower leaves (three to five feet from the ground) and the herbaceous and low shrubby plants are probably not different.

4. This investigation indicates that the standard water-vapor loss of a species is not necessarily correlated with the position of a species in a relative scale of xerophytism, as indicated by the usual habitat of that species. Many xerophytic species exhibit relatively high rates of water-vapor loss, while *vice versa*, many mesophytic species have low rates.

5. Evidence is presented which indicates that plants growing in soil saturated with water and poorly aerated, such as in bogs and swamps, have lower rates of water-vapor loss than many growing in drier habitats, often approaching those of xeric situations. Internal physiological conditions and poorly developed root systems may be the causes.

6. For most species the time of maximum water-vapor loss occurs during the morning hours, long before the time of maximum evaporation. A frequency curve, constructed from these maxima, shows that 93% of the 148 plants studied, have their maximal water-vapor loss between 7:00 A. M. and 12 M., over 89% between 7:00 and 11:00 A. M., and 52% between 9:00 and 10:00 A. M. The greatest number of maxima occurred about 9:00 A. M., regardless of whether the habitats were wet or dry.

7. Pronounced periodicity of water-vapor loss occurred from the stomatal surfaces of nearly all species.

8. The majority of plants investigated showed a water-vapor loss of 0.3 g. per sq. dm. of leaf surfaces free of stomata.

9. When the same species was studied in two or more habitats the rate and the curves were usually different.

10. The lower leaves of *Fagus* and *Carya* had greater water-vapor loss than those at higher levels.

REFERENCES

(1) **Bakke, A. L.** Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. Jour. Ecol., 2: 145–173. 1914.
(2) **Blaydes, G. W.** A survey of rates of water loss from leaves. Ohio Jour. Sci., 28: 99–118. 1928.
(3) ———The cobalt chloride hygrometric paper and weighing methods of measuring water loss. In press, Ohio Jour. Sci.
(4) **Gray, Asa.** New manual of botany, 7th ed. American Book Company, New York. 1908.
(5) **Livingston, B. E.** The resistance offered by leaves to transpirational water loss. Plant World, 16: 1–35. 1913.
(6) ———and **Shreve, Edith B.** Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. Plant World, 19: 287–309. 1916.
(7) **Meyer, Bernard S.** The measurement of the rate of water-vapor loss from leaves under standard conditions. Amer. Jour. Bot., 14: 582–591. 1927.
(8) **Pool, Raymond J.** Xerophytism and comparative leaf anatomy in relation to transpiring power. Bot. Gaz., 76: 221–240. 1923.
(9) **Sayre, J. D.** The relation of hairy leaf coverings to the resistance of leaves to transpiration. Ohio Jour. Sci., 20: 55–86. 1920.
(10) **Stahl, E.** Einige Versuche ueber Transpiration und Assimilation. Bot. Zeitung, 52: 117–146. 1894.
(11) **Whitfield, Chas. J.** Ecological aspects of transpiration II. Pike's Peak and Santa Barbara regions: Edaphic and climatic aspects. Bot. Gaz., 94: 183-196. 1932.
(12) **Wilson, H. W.** Studies on the transpiration of some Australian plants. Proc. Roy. Soc. Victoria, 36: 175–237. 1924.

Geologic Structures

In 1923 Bailey Willis wrote the first edition of "Geologic Structures" and used some 295 pages to describe them and to interpret them. The second edition appeared in 1929 and a third revised edition in 1934. This last edition gives within useful limits a complete treatment of the subject. In sixteen chapters and four appendixes the two authors consider geologic structure. The chapters in order take up Problems of Rock Deformation, *Mechanical Principles*, Stratified Rocks, Flexures and Folds, *Analysis of Folds*, Division of Rocks by Joints, Description of Faults, *Fault Types and Fault Displacements*, *Analysis of Faulting*, Structures of Igneous rocks. Structures of Metamorphic rocks, Physiographic Expression of Structure, Field Methods, *Graphic Methods*, *Practical Problems*, and Fundamental Facts and Concepts. The headings in italics are more technical than the others. The appendices are mainly technical discussions of various aspects of structure or experimental work on folds.

Students of geology will find considerable food for thought contained in the 509 pages. For those not primarily interested in structure it is an excellent hand book. Essentially it is a textbook for systematic study of structure.

—WILLARD BERRY.

Geologic Structures, by Bailey Willis and Robin Willis. xviii+544 pp. New York, McGraw-Hill Book Co., 1934. $4.00.